

Fixed points and stability (3505 Population genetics)

1. Compute all fixed points and check their stability for the selection model with

$$W = \begin{pmatrix} w_{11} & w_{12} & w_{13} \\ w_{21} & w_{22} & w_{23} \\ w_{31} & w_{32} & w_{33} \end{pmatrix}$$

Solution. Recall that the state of the population is described by the vector of frequencies (p_1, p_2, p_3) with $p_1 + p_2 + p_3 = 1$ and $p_i \geq 0$, $i = 1, 2, 3$. Also recall that the frequencies in the next generation are given by

$$p'_i = \frac{p_i(Wp)_i}{\bar{w}}, \quad i = 1, 2, 3.$$

Here

$$(Wp)_i = w_{i1}p_1 + w_{i2}p_2 + w_{i3}p_3,$$

and

$$\bar{w} = w_{11}p_1^2 + w_{22}p_2^2 + w_{33}p_3^2 + 2w_{12}p_1p_2 + 2w_{13}p_1p_3 + 2w_{23}p_2p_3$$

is the mean fitness in the population.

At the fixed points, where $p'_i = p_i$, we thus have $(Wp)_i = \bar{w}$ for all i with $p_i \neq 0$ (and, hence, $(Wp)_i = (Wp)_j$ for all i and j for which $p_i \neq 0$ and $p_j \neq 0$).

There are three steps to find the fixed points:

- (a) Monomorphisms. The points $F_1 = (1, 0, 0)$, $F_2 = (0, 1, 0)$, and $F_3 = (0, 0, 1)$ are always fixed points. Note that even if, for example, $w_{11} = 0$, the point $F_1 = (1, 0, 0)$ is a fixed point.

- (b) Partial polymorphisms. These points can be found as follows.

The fixed point with $p_1 = 0$ or $F_{23} = (0, p_2, p_3)$ can be found from the conditions $(Wp)_2 = (Wp)_3$ and $p_2 + p_3 = 1$. That is, from the conditions: $w_{22}p_2 + w_{23}p_3 = w_{32}p_2 + w_{33}p_3$ and $p_2 + p_3 = 1$, where we have used that $p_1 = 0$.

The fixed point with $p_2 = 0$ or $F_{13} = (p_1, 0, p_3)$ can be found from the conditions $(Wp)_1 = (Wp)_3$ and $p_1 + p_3 = 1$. That is, from the conditions: $w_{11}p_1 + w_{13}p_3 = w_{31}p_1 + w_{33}p_3$ and $p_1 + p_3 = 1$, where we have used that $p_2 = 0$.

The fixed point with $p_3 = 0$ or $F_{12} = (p_1, p_2, 0)$ can be found from the conditions $(Wp)_1 = (Wp)_2$ and $p_1 + p_2 = 1$. That is, from the conditions: $w_{11}p_1 + w_{12}p_2 = w_{21}p_1 + w_{22}p_2$ and $p_1 + p_2 = 1$, where we have used that $p_3 = 0$.

It might happen that some or all of these equations cannot be solved for $p_i \geq 0$, and then there are no fixed points for the corresponding partial polymorphisms.

- (c) Complete polymorphism $F_{123} = (p_1, p_2, p_3)$. The possible fixed point can be found from the set of equations $(Wp)_1 = (Wp)_2 = (Wp)_3$ (two independent equations!) and $p_1 + p_2 + p_3 = 1$. For example, one can solve:

$$w_{11}p_1 + w_{12}p_2 + w_{13}p_3 = w_{21}p_1 + w_{22}p_2 + w_{23}p_3$$

$$w_{21}p_1 + w_{22}p_2 + w_{23}p_3 = w_{31}p_1 + w_{32}p_2 + w_{33}p_3$$

$$p_1 + p_2 + p_3 = 1$$

It can happen that there are no solutions satisfying $p_i > 0$ for all $i = 1, 2, 3$. Then there are no fixed points among complete polymorphisms.

Next, one should check the stability for the fixed points found. This can be done as follows:

- (a) Monomorphisms. Consider, for example, the point $F_1 = (1, 0, 0)$. This point will be asymptotically stable if and only if $w_{11} > w_{12}$ AND $w_{11} > w_{13}$.
- (b) Partial polymorphisms. Suppose, for example that $F_{12} = (p_1, p_2, 0)$ is a fixed point. It is internally asymptotically stable if $w_{12} > w_{11}$ and $w_{12} > w_{22}$. However, for stability we also need external stability — against the invasion from the third allele. So additionally we need that $(Wp)_1 = (Wp)_2 > (Wp)_3$, computed at the fixed point. Then the fixed point is also externally stable. It is unstable if any of the inequalities is reversed (some more subtle analysis is required in the borderline cases). The cases of the fixed points on F_{13} and F_{23} can be dealt with analogously.
- (c) Complete polymorphism, or the internal fixed point. In this fixed point the mean fitness \bar{w} is equal to any of $(Wp)_i$. If any of the points above (in (a) and (b)) are stable, the internal fixed point is unstable. If all other fixed points are unstable, the internal fixed point will be stable (except for degenerate cases). To check the stability one can also compare the mean fitness $\bar{w} = (Wp)_i$ with the values of fitness in other fixed points. The fixed point with the strictly largest fitness is always asymptotically stable.